

VIII.—On the Tribe Colletieæ, with some Observations on the Structure of the Seed in the Family of the Rhamnaceæ. By JOHN MIERS, F.R.S., F.L.S. &c.

THIS tribe differs from others of the *Rhamnaceæ* in having always opposite branchlets usually terminating in acute spines, while in most Rhamnaceous genera they are alternate; for, though they sometimes approximate in pairs, they are never exactly opposite: the same may be said of their leaves. The *Colletieæ* also differ in the position of their petals and stamens, their insertion being always perigynous upon the tube of the calyx at some distance from the hypogynous disk, which in *Colletia* assumes a perigynous form: in this respect we meet with only one exception, in *Adolphia*, where, owing to the extreme shortness of the calycine tube, their point of attachment is drawn close to the disk; but, although thus brought into proximity, they are not actually inserted upon its margin, as they are generally in the *Rhamneæ*. In the tribe *Gouanieæ*, so different in most other respects, the insertion of the petals and stamens is like that of the *Colletieæ*. The stamens are placed opposite to as many scale-like petals in all the *Rhamnaceæ*; they are generally concealed and hooded by them in the *Colletieæ*, and are inserted upon their claws, between the lobes of the calycine border; the petals are, however, sometimes wanting, and in a single apetalous species the insertion of the stamens is below the middle of the tube. The *Colletieæ*, besides, are generally distinguishable at a glance by their peculiar habit: the branchlets, half abortive, often assume the form of spines, which are either quite bare, or they are foliiferous, or else they become more elongated, bearing both leaves and flowers, but sometimes they are destitute of both, with a broom-like appearance; the leaves, when present, are always small and opposite, or, by the approximation of the axils, almost fasciculated, and are either entire or denticulated, and sometimes are reduced to almost obsolete proportions. Most of the species at present known are natives of South America; there are a few in Mexico, one from the Galapagos, one from the island of Juan Fernandez, one from Australia and Tasmania, and another from New Zealand. There has hitherto been much confusion among the genera, the characters of many of them being still undefined: thus *Trevoa* and *Talguenea*, which I proposed above thirty years ago, have been confounded together by most botanists. My observations, I hope, will enable me to define the characters and limits of these as well as the other genera of the tribe.

When Jussieu published his 'Genera Plantarum' (in 1789), the only genus then known of the present tribe was *Colletia*; it

was there placed in his order *Rhamni*, a heterogeneous group composed of *Rhamnaceæ*, *Celastraceæ*, *Aquifoliaceæ*, *Bruniaceæ*, *Staphylaceæ*, and some other genera. From this association Mr. Brown (in 1814) separated the *Celastraceæ*, including the *Aquifoliaceæ*, and (in 1818) the *Bruniaceæ*; and thus circumscribed, DeCandolle (in 1825) published an enumeration of the order, wherein *Colletia* appears as the only genus belonging to the tribe since constituted. We owe to Brongniart (in 1826) the best monograph of the family that has yet been published, where its affinities are well discussed, and where ample characters of the genera are given: here he first separated *Retanilla* from *Colletia*, and at that time he was able to muster only seven species in these two genera. Subsequently to that period, the number of plants belonging to the *Rhamnaceæ* have become greatly multiplied, and the characters of the species better known; several new genera have been established, but no regular enumeration has appeared since that of Brongniart above mentioned, so that a proper monograph of the order has become a great desideratum. It seems that Reissek (in 1840) was engaged in this important task; but his promised monograph, after a lapse of twenty years, has not yet made its appearance. Endlicher, in the same year, however, adopted the arrangement of Reissek, and accordingly, in his 'Genera Plantarum,' divided the family into six tribes, the *Colletieæ* being one of them, which there comprehends six genera.

Before I proceed to arrange my own observations, I will offer a few prefatory remarks upon many points of structure that I have met with in this family, and which do not appear to have been noticed. These developments I have found in all the species of the *Colletieæ* that have come under my scrutiny; they are constant in the *Gouanieæ*, and have been observed in many genera of the *Rhamneæ*; but I have not attempted a general examination of the whole order, as this required more time than could be devoted to it, and would have drawn my attention from other investigations in which I have been long engaged.

The fruit in all the genera of the *Colletieæ* is polycarpous, the normal number of its cells being three, rarely four: these are sometimes reduced to two, even in the ovary; and if the fruit be occasionally monospermous, as often occurs in *Trevoa*, *Colletia*, &c., the vestige of each abortive cell is always distinctly visible. The ovules are invariably solitary in each carpel, always erect, and fixed in the bottom of each cell; the radicle of the embryo constantly points to the hilum.

The seeds throughout the whole tribe of the *Colletieæ* present the same features; and as there are many curious circumstances

connected with their structure, those of *Colletia dumosa*, collected by me in Chile thirty-five years ago, are selected as an example. They are of an oval form, about $1\frac{1}{2}$ line long, 1 line in diameter, sometimes slightly compressed, often with an obsolete ridge on the ventral face, which has been mistaken for a raphe; erect; with a very hard polished outer surface, appearing finely granulated when magnified: this outer coating is corneous in texture, becoming softer by long maceration, when it may be cut through with a sharp knife; it is somewhat translucent, but rendered densely black by the lining that adheres to it; at its base, in a transverse direction in regard to the fruit, is seen a long furrow, or compressed bilabiate slit, which is always pervious. This outer shell is uniform in thickness, homogeneous in texture throughout, and under the microscope is seen to be composed of numerous narrow, transverse, hyaline cylinders, apparently solid, of equal size, all placed in a direction radiating from the centre of the seed; so that when the shell is viewed through either of its faces, it appears like a reticulation of minute hexagonal cells, each cell corresponding to the end of a long cylinder: these cylinders, by long maceration, may be separated from each other; it is clear, therefore, that in this organization there is not the slightest approach to any longitudinal vascular continuity. For reasons to be shown presently, we may infer that this shell is not one of the ordinary integuments developed from any of the original tunics of the ovule, but of posterior growth, and therefore not a testa, as hitherto supposed: it is a production apparently analogous in its structure to the outer tunic formerly described in the seeds of *Cucurbitaceæ**.

* Trans. Linn. Soc. xxii. 92 & 108. More extended observations upon the seeds of different *Cucurbitaceæ* have led me to modify the inference made in that stage of the inquiry (*loc. cit.*), that the more external covering (there described as formed of three several portions) consists of epiderm, mesoderm, and endoderm—terms incorrectly applied to parts evidently distinct in their origin. The outer very thin stratum of that fleshy covering is reticulated with long hexagonoid cells, and its origin may be traced to an extension of the outer membrane of the funicle; the intermediate soft substance is a collection of lax fleshy cells intermixed with numerous araneiform filaments, all probably emanating from the fleshy substance of the funicle. In many genera this fleshy parenchymatous substance is entirely wanting, so that the shell of the seed is covered simply by the above-mentioned thin pellicular membrane. In the centre of the funicle a thick cord of vessels is seen, which, as it approaches the seed, is observed to bend towards one side, and to enter one of the ends of the linear basal slit of the hard tunic; there is no appearance of its bifurcation at that point, as the vessels of the funicle appear to be immediately connected with only one of the two extremities of the peripheral raphe, which meet together in the base of that tunic. This hard crustaceous shell, usually called the testa, presents no sign of any organic connexion with the two layers of structure before mentioned, nor with the more internal tunic. The exist-

Within this shell, and adhering to it, is a second tunic, which is membranaceous, and agglutinated to it by means of a thick layer of cellular deposit of spongiöse texture, brittle when dry, and so loosely aggregated that, when removed and soaked in water, and then slightly touched, these cells separate into distinct globules of a hexagonoid shape, and of a deep crimson colour. In the substance of this second membranaceous tunic is observed a white cord, which rises from the bottom, originating in one of the angles of the basal pervious chink, runs up one side of the tunic, crosses its summit without interruption in its course, and passes down the contrary side, terminating in the opposite corner of the basal perforation, and thus making a complete peripheral circuit round the inner surface that lines the shell. This cord is composed of a number of delicate spiral threads, so free that each fibre is easily drawn out separately. In some genera of the *Rhamnaceæ* (as in *Zizyphus*, *Alphitonia*, &c.), this second tunic is perfectly free from the outer corneous shell, a considerable space existing between them, in which is generally found a small quantity of very lax white cellular tissue. A third integument, although free from it, fills the space in the upper moiety of the last-mentioned coating in *Colletia*, but a little below the middle it becomes gradually narrower, more opaque, and of a thicker texture, until it tapers into a short stout thread, that terminates in the basal perforation of the outer shell. The opposite extremity, or summit, is marked with a dark fleshy disk, like a chalaza, of nearly its own diameter. These integuments closely invest the albumen, which is fleshy, homogeneous in texture, and of considerable thickness on the ventral and dorsal faces, but becomes very thin round the margins of the cotyledons, the whole mass being of a roundish oval shape, suddenly contracted at its base into a prominent nipple, which is enclosed within the rostellated neck of the investing integuments before described; the embryo is nearly the size of the albumen, and much flattened, the cotyledons being oval, foliaceous, and fleshy, slightly cordate at the base, where they are united by a short cylindrical radicle,

ence of a small thickening or chalazal spot on the summit of the inner integument, and of another round its contracted basal neck, are constant in all the seeds I have examined. The raphe is invariably peripheral, and undisturbed in its course by the apical chalaza, which it crosses: it is also free from the shell in all parts, except at its two basal extremities, which are both imbedded in channels formed in the crustaceous thickening of the shell around its base; but one of these extremities only, as just said, appears to be a continuation of the cord of the funicle. The imbedding of the two extremities of the raphe in a crustaceous deposit in the base of the shell is analogous to the structure observed in many genera of the *Rhamnaceæ*.

one half of which lies within the sinus, the other half in the nipple of the albumen; the cotyledons are anterior and posterior in regard to the axis of the fruit.

The presence of the distinct external crustaceous shell, always more or less pervious at the basal extremity (or one of its sides), and the position of the raphe, as above described, attached to an intermediate integument, making nearly a complete circle round the seed,—are features that occur not only in all the *Colletieæ*, but in all the genera of the *Rhamnaceæ* that I have examined, though subject to several modifications, which I will mention. In *Rhamnus catharticus*, however, as well as in *R. Alaternus* and a few others, the raphe, though still peripheral, is differently situated, for it is everted yet further from the position mentioned in *Colletia*; it is seen upon the dorsal face of the seed,—a well-known occurrence, that has been ingeniously accounted for by Mr. Bennett*; but before we adopt his conclusion, it is desirable to investigate the circumstances attendant on the phenomenon. Mr. Bennett says that he has universally found, throughout all *Rhamnaceæ*, that the ovules, in their early state, uniformly exhibit a ventral raphe; and hence he infers that any variation subsequently observed in its relative position, whether it be shifted to one side or round to the dorsal face, must be due to a simple twisting of the funicle, by which the ovule is turned upon its axis, either to the extent of a quarter or of half a revolution. Were this explanation required only in the case of the raphe becoming dorsal, we could scarcely refuse our assent to it, because in that case it appears to solve the difficulty with apparent satisfaction, notwithstanding that Mr. Bennett confesses his inability to assign any cause for so singular a rotation of the ovule.

The first point to be considered is the soundness of the foundation of the argument, that at the period of its fertilization the ovule has its raphe directed to the ventral side, and that it subsequently turns away from it by a lateral torsion of its funicle. Mr. Bennett states (*loc. cit.* p. 131) that he has invariably found this to be the case in the *Rhamnaceæ*; and this statement has been accepted as an indisputable fact by nearly all botanists. Some few, however, have ventured to cast a doubt on the subject: Mr. Clarke† says he has always found the raphe dorsal or lateral in that family from an early period; while Prof. Agardh affirms the reality of this latter circumstance, and protests in positive terms against the prevalent belief on this subject‡; in his work above referred to, he gives a figure as an example of

* *Plant. Jav. rar.* 131.

† *Linn. Proceed.* ii. 143–150; *Ann. Nat. Hist.* ser. 2. xi. p. 85.

‡ *Theor. Syst. Plant.* p. 178, and plate 15. fig. 5.

the structure (plate 15. fig. 5) where the raphe is turned away from the axis of the ovary prior to its impregnation. My own observations upon this point, though limited, certainly favour the latter view; for I have found, in repeated examples of *Rhamnus chlorophorus* where the raphe in the ripe seed is half lateral, half dorsal, that, in its unimpregnated ovule, it occupies exactly the same position: had there been any previous pivoting round upon its funicle in this case, the micropyle would have been turned away from the point necessary to its fertilization, and the funicle would consequently have intervened between the foramen of the ovule and the impregnating point protruding from the placenta; but I found, on the contrary, that the micropyle is placed over the fascicle of stigmatic tissue, evidently in its normal and proper position. Another confirmation of the same view occurs in *Rhamnus Alaternus*, where, in the ripe seed, the raphe is exactly dorsal, as in *R. catharticus*: here I found the unimpregnated ovule having its raphe precisely in the same position as in the seed, with its micropyle placed over the impregnating point of the placenta, and situated between the funicle and the axis of the ovary, proving that in this case there had been no twisting of the funicle, and consequently no pivoting of the ovule. I have also examined the living ovary of *Rhamnus catharticus* in an extremely young state, long before the ripening of the anthers, and therefore prior to its impregnation, and I have found the raphe most distinctly upon the dorsal face, precisely in the same position which it occupies in the ripe seed. All the evidence that I have thus been able to collect tends therefore to subvert Mr. Bennett's hypothesis. On the other hand, the explanation I have offered on a former occasion*, of the cause of a dorsal or lateral raphe occurring, as I believe it does, universally throughout the *Rhamnaceæ*, appears to me quite satisfactory: here, from a most simple and natural cause, originating either in the epipylar or allopylar pullulation of the nascent development from the basal placenta, we have the ovule either with a dorsal or lateral raphe; and, where dorsal, it is forced into that averse position by the mere act of the resupination of the ovule owing to the pressure of its growth against the base of the cell, in the manner first sagaciously suggested by Mr. Brown in the case of *Euonymus*. Had the same epipylar pullulation originated out of a higher point of the axis of the ovary, we should have seen in that case a pendent ovule with a ventral raphe, as occurs in the neighbouring family of the *Celastraceæ*, where in the same cell, from the cause here assigned, we sometimes meet with ovules, some with a ventral and others with a dorsal raphe.

* Ann. Nat. Hist. 3 ser. iv. 25.

I will now advert to the other anomalous fact, in regard to the raphe, above alluded to. Botanists have always attributed to the seed of *Rhamnus* a chartaceous testa, with a raphe as a simple cord, that runs up its external face, or along one side, in a deep groove formed by a conduplication of the whole seed, and then terminates in the apical chalaza; but one important circumstance connected with this structure has been altogether overlooked. I have found that this cord has a peripheral range similar to that in *Colletia*, with this difference, that instead of running laterally round it in the line of the margins of the cotyledons, it is directed along the middle of one cotyledon, in a deep groove upon the dorsal side, then crosses over the chalaza without any apparent interruption in its course, and returns down the ventral side in a direction close to the median line of the other cotyledon, till it again reaches the hilum.

As this structure is at variance with recorded descriptions, it is necessary to state the circumstances more in detail. My first observations were made upon the dried seeds of *Rhamnus catharticus*: this seed is smooth, of a hepatic brown colour, and of a flattish oval shape, somewhat tapering to the base, where it is callous and more polished; it is a little angular upon the ventral face, and rounded upon the dorsal side, along which is seen a line running from the apex to the base: on pressing it, this line is found to be the margin of a deep chink, which extends all the way down to the axis of the seed. If we carefully remove the outer coating, we find it rather thin, very brittle, and crustaceous, thus exposing a second tunic, which is very fine in texture, membranaceous, and polished, and upon its ventral side, opposite to the dorsal chink, is seen a distinct line running from the base to the apex, where it passes over a large areolar disk, and runs into the summit of the chink in continuity with the main cord of the raphe. If we take another seed, and cut it in two transversely, we see the outer brittle tunic just mentioned becoming somewhat thicker as it approaches the dorsal chink, where it is continued by induplication, in the form of two rather thick crustaceous plates that line the sides of the chink, the internal edges of these plates being quite disconnected with each other: it is evident, therefore, that this outer covering is not an entire tunic; for if it were unfolded, it would be found to be merely a thin plate with thick margins, which are introflected in the manner described. In the bottom of the chink, which widens towards the axis, is seen a thin membranaceous diaphragm, that forms one side of a square hollow cavity which runs through the axis from the apex to the base, and which diaphragm is found to be a portion of the second thin polished membranaceous tunic before mentioned, that lies beneath the

outer crustaceous covering; and upon this diaphragm is observed the thick cord described by botanists as the dorsal raphe, which rises from the base, crosses the disk-like areole in the summit, and runs down the opposite side of the seed, forming the line first described as seen on the ventral face. The whole of this intermediate integument, with its entire raphe, may be exposed to view if we chip away in small fragments the outer crustaceous coating with the point of a knife, when the two cords, both ventral and dorsal, are distinctly seen; the two teguments are closely adpressed upon each other, except over the ventral cord, where there is always a considerable interval between them, thus showing that the raphe has no connexion whatever with the outer crustaceous coating. Beneath the second envelope is a third integument, which immediately invests the albumen, and which is thin and membranaceous; these two integuments, though free, are in immediate contiguity at all parts of their surface, except along the middle of the dorsal face, where they become separated to form the square hollow channel in the axis above-mentioned, one side of which square, with the imbedded raphe, is formed by the induplication of the intermediate integument. The embryo is broad and foliaceous, and is covered by a layer of fleshy albumen, equal in thickness to the cotyledons,—the margins of the whole, together with the enveloping tunics, being conduplicated into the hippocrepical form at first described. We see here, therefore, the existence of three seminal envelopes, very similar in their nature to those described in *Colletia*, with this remarkable difference, that in the latter the crustaceous coating is entire, while in *Rhamnus* it is always incomplete upon one side. In *Rhamnus catharticus* the groove formed by the conduplication of the seed is generally in the middle of the dorsal face, though sometimes nearly lateral, caused by unequal growth, in consequence of the partial abortion of one of the carpels; but in all these cases, the two lines of raphe always correspond with the middle of the cotyledons, while in the *Colletia* they constantly run along their margins*.

The same structure exists in *Rhamnus Alaternus*; but on account of the small size of its seeds, and the greater tenuity of the several integuments, it requires much care to dissect the parts. The crustaceous covering is very thin, and adheres more firmly to the extremely delicate intermediate integument, and it is therefore difficult to separate them without lacerating the latter; but when the separation is made with care, we find the ventral portion of the cord imbedded like a white line in that distinct integument, and running from the apex to the base:

* Analytical details of this structure in *Rhamnus catharticus* will be shown in plate 33 A of the 'Contributions to Botany.'

the dorsal groove is more shallow, and embraces the other corresponding portion of the raphe and integument, so that, on detaching the external crust, the raphe comes away with it, tearing itself from the rest of the integument*.

This structure is repeated, under somewhat varied circumstances, in *Rhamnus chlorophorus*, Dene. : here, however, the raphe is lateral, not dorsal; the cotyledons are not involutely inflected, as in the former case, but are simply complicated or folded upon one another, so that their midribs stand opposite one margin of the seed, while all the four edges of the two cotyledons face the contrary margin, the albumen and integuments partaking of the same complicature. A deep groove is thus formed, reaching to the axis, as in *R. catharticus*, which here is therefore lateral, instead of dorsal; the raphe does not lie in the bottom of the deep groove, as in the latter species, but as it leaves the chalaza it runs along the mouth of the groove from top to bottom, as in *R. Alaternus*, and the middle integument, to which it is attached, here makes a deep plicature which nearly reaches the bottom of the groove; and throughout the whole length of this plicature it is separated on both sides, by a vacant interval, from the inner integument, thus forming a kind of loose, incomplete partition all down the groove. This intermediate tunic is membranaceous, and invests all other parts of the seed; it is enclosed within an external, hard, polished, testaceous covering, similar in texture and appearance to that in *R. catharticus*, but it is not, as in that species, inflected into the groove: the groove is here rather an open slit, always on the sinister margin (looking from the axis of the fruit), and is surrounded by a thick callous rim, which, rising from the basal and hilar point of attachment of the seed, extends upwards to one-third or half its length. This crustaceous coating lies close upon the intermediate integument of the seed over its two broad faces; but at its summit, and all along the other margin (opposite to that of the groove), a vacant space intervenes between them. The raphe is imbedded in that intermediate integument in the form of a simple cord, the thicker moiety of which runs along the base of the groove, and is free from it at all points, except at the bottom of the groove, where it adheres to it by means of a crustaceous deposit: it continues its course in a peripheral direction, crossing the apical chalaza beneath the free space mentioned, and runs down along the opposite margin of the seed, till it again reaches the pointed base or micropylar extremity of the inner integument. I have frequently succeeded in detaching the entire raphe with a portion of the integument

* This structure will also be given in detail in plate 33 c of the 'Contributions to Botany.'

in which it is imbedded (even from over the chalaza), when it thus appears in one unbroken peripheral band, containing spiral vessels: this separation of the raphe may be effected without disturbing the under or more internal integument, showing that it has no adhesion to it*.

A very similar structure is found in *Rhamnus utilis*, Dene.: here the embryo, the albumen, and the two integuments, are folded on one another exactly as in *R. chlorophorus*, the groove being, in like manner, constantly on the same sinister margin; the testa also shows, on the dexter margin of the seed, a similar continuous cord of the raphe; but the intermediate integument, in its plicature within the groove, adheres on both sides to the inner tunic, till it arrives nearly at the bottom of the channel, where it suddenly separates from it, and crosses the groove in form of a diaphragm, leaving a vacant square space in the axis, formed by a separation of the integuments, which extends from the apex to the base, and upon this diaphragm is distinctly seen the main cord of the raphe,—an organization similar to that of *R. catharticus*. The outer coating is of the same form as in *R. chlorophorus*, but of a different texture; it has the same longitudinal open slit along the lower half of the sinister margin, but its edges are more or less inflected into the groove. Its texture is not crustaceous, but consists of a thick simple membrane, invested with a number of compact long yellow cells, disposed horizontally, and aggregated into a lax spongiöse covering, which sometimes partially adheres to the endocarp.

In *Frangula vulgaris* the structure is different from that of *Rhamnus*, even when the raphe is lateral, as I have shown it to be sometimes, in the latter genus. The seed is nearly orbicular and much flattened; the crustaceous covering is as thin and delicate as in *Zizyphus*, but its basal foramen is much larger, rounder, and more open, with two thick callous lips placed right and left of the axis, not anterior and posterior, as in that genus and in *Colletia*. Beneath it, and lying between it and the intermediate integument, there is a deposit like charred paper, which in most parts adheres to the external crust, but is separable from it, as in *Colletia*. On removing this, we find the very delicate intermediate membranaceous integument conical towards the base, where it terminates in a hooked thread, as in *Colletia*, and from which, right and left, along each margin, is seen a thick white cord, both arms being joined in one peripheral line over the apical chalaza. It will be remarked that, upon the sinister side looking from the

* Complete details of this organization will be given in plate 33 B of the 'Contributions to Botany.'

axis, the cord is thicker and enveloped in a yellowish incrustation, which, for one-third the length of the seed, there adheres to the outer crustaceous coating, as was observed in *Rhamnus chlorophorus*. The embryo is perfectly flat; the cotyledons very thin and foliaceous, enclosed in an albumen of equal thickness; the two internal integuments are of extreme tenuity, and on that account are not easily separated. This organization, it will be seen, greatly resembles that of *Zizyphus**.

In *Zizyphus*, I find the course of the raphe also peripheral, but it runs along the lateral edges opposite the margins of the cotyledons, as in the *Colletieæ*; and we find here some points of structure deserving of being recorded. The outer corneous covering of the seed is entire, as in the *Colletieæ*, but much thinner in texture, and more translucent. This coating is of a more compressed form, tapering towards the base, which is polished and somewhat tumescent, and which has a basal chink similar to that of the *Colletieæ*, through which the nourishing vessels of the raphe pass from the placenta. It may here be observed, that in the bottom of each cell of the nut is seen a small fleshy cup, with a crenulate raised border, within which the seed is seated, and across the bottom of this cup is a white raised line, corresponding to the hollow in the basal chink of the seed; but the margins of this chink and the tumid base of the external coating are highly polished, and the latter shows no sign of any organic connexion with the cup: the hilar point of attachment is therefore confined to the mere cord of vessels proceeding from the placenta to the raphe. The second tunic, which is very thin and membranaceous, does not quite fill the cavity of the outer shell; it is more conical at its base, where it terminates in a short thread that issues through the chink above mentioned; the space between it and the outer shell is filled with a quantity of very lax white cellular tissue; it is pyriform in shape, much compressed, and tapers into a short cord at its base, which is seen to divide itself into two prominent threads that run along the margins of the tunic, and meet over a large fleshy chalazalike disk in the apex, in one uninterrupted line: this cord of vessels is therefore completely peripheral, as in *Colletia*. This second tunic is quite free from a third, inner integument, which is thicker and more opaque, and which invests a very thin fleshy albumen: this third integument is sensibly shorter, and more conical at its base, where it terminates in a dark areolar neck, and tapers into a short suspensor-like thread, which is embraced by the neck of the second tunic. These two integuments are easily separable from one another by the introduction of a needle

* This structure will be fully shown in plate 33 D of the 'Contributions to Botany.'

between them, except round the margin of the apical chalazal disk, where they appear to be intimately agglutinated; the embryo is flat and compressed, its foliaceous cotyledons being parallel with the partition of the nut, and their margins contiguous to the peripheral cord of the raphe. This organization* is more evidently seen in this instance, as the seed is six times longer than that of *Colletia*, which it greatly resembles in structure: it is also remarkable for exhibiting many points analogous to the organization I have described in the seeds of *Cucurbitaceæ*†.

This singular extension and displacement of the raphe, accompanied by the formation of an extraneous crustaceous covering in the seed, was not altogether a novel fact, as I thought when I first remarked it in the *Cucurbitaceæ*; for the occurrence was partly noticed thirty years ago, in *Rhamnus*, by Brongniart, who, strangely enough, was not struck by the appearance of so remarkable a phænomenon, which he passed over without comment, and it has remained unnoticed by other botanists since that time. Brongniart's words are worthy of being quoted, as showing a notable correspondence with my observations. Alluding to the *Rhamnaceæ*, he says ‡: "Dans toutes ces plantes, le test lui-même, examiné au microscope sur des ovules déjà fécondés et à moitié de leur développement, est composé de trois couches très différentes; l'une, externe, n'est qu'un epidermis mince §; l'autre, moyenne, est solide et fibreuse, formée de fibres ou cellules allongées transversales, c'est elle qui doit former le test de la graine; enfin l'interne, très épaisse dans les premiers temps qui suivent la fécondation, est formée de parenchyme lâche, composé de cellules remplies de globules verts; elle s'atrophie, peu-à-peu, à mesure que l'amande et l'embryon se développent. C'est en général dans cette couche que passent les vaisseaux nourriciers, qui composent le raphé, et vont former la chalaze, raphé qui dans ce cas, suit l'un des côtés de l'ovule en dedans du test, et redescend en partie de l'autre côté, après que la plupart des vaisseaux qui le composent, ont donnés naissance par leur épanouissement à la chalaze." The latter conclusion appears, however, to have been only conjectural||.

The entire peripheral circuit of the tracheal vessels in one

* Drawings of this analysis will be given in plate 33 E of the 'Contributions to Botany.'

† Linn. Trans. xxii. 92.

‡ Ann. Sc. Nat. x. 340.

§ This is a thin layer of cellular tissue that invariably lines the epicarp, and partially adheres to the outer crustaceous coating of the seed in *Rhamnus*, and which I have not considered necessary to mention in the preceding description.

|| "La chalaze vasculaire m'a toujours paru formée entièrement par une épanouissement des vraies trachées: elle est formée extérieurement par une expansion des vaisseaux du raphé" (*l. c.* p. 341).

of the integuments of the seed, which I have invariably found in one unbroken continuity, was therefore not fully traced by that eminent botanist, although it is evident, from the above quotation, that he had noticed the return of the raphe over the chalaza, and its partial descent down the contrary face of the seed. It is strange that this remarkable and novel feature was not afterwards alluded to, and that the mention of this extension of the tracheal vessels is omitted in the very copious diagnosis he gives of the order, where every other circumstance connected with the structure is carefully enumerated.

Some indications, leading to a knowledge of the origin of the external crustaceous envelope of the seed in *Rhamnaceæ* may probably be drawn from Brongniart's valuable memoir above quoted, in which he records the changes which he observed during the periods of the impregnation and growth of the ovule in that family. These details were published in 1827, a year or two prior to the appearance of Mirbel's two celebrated memoirs on the development of the vegetable ovule, and before the modern nomenclature of the parts of the ovule and seed was adopted. I will therefore briefly recapitulate such of his observations as bear upon the subject under consideration. He noticed* that the stigmatic tissue terminated in a small cellular protuberance (since denominated the "telæ conductrices") in the inner angle of the cell of the ovary, close to the foramen of the anatropous ovule; and he remarked the condition under which the latter became fecundated: the ovule is always supported upon a somewhat elongated funicle filled with nourishing vessels, and surrounded by loose cellular tissue; this funicle, which is very contracted before impregnation, begins to swell from the moment that the stigma has received its fertilizing influence; it afterwards expands and extends itself over the foramen of the ovular tunic. Brongniart, who first traced the expansion of the boyaux of the pollen-grains, and their passage down the stigmatic channels†, was not then aware of their ultimate extension through the prominence he observed at the termination of those channels; nor did he notice the continuity of one of these boyaux with the minute thread which he had remarked in connexion with the embryo-sac, and which he considered to be an emanation from its neck: according to the notion he then entertained, he concluded that the act of impregnation was conveyed through the agency of the cellular tissue of the umbilical cord‡, which the fact he recorded of the swell-

* Ann. Sc. Nat. x. 340.

† Ib. xii. 152 & 256; read before the Academy Dec. 26, 1826.

‡ Ann. Sc. Nat. x. 343: "Et c'est par l'intermédiaire de ce tissu cellulaire du cordon ombilical que je pense que s'opère l'impregnation de

ing of the funicular support, and its subsequent extension over the coats of the ovule, seemed to support. I now call attention to this last-mentioned circumstance, because it may serve to explain some essential points of structure in the seeds of the *Rhamnaceæ*, and may enable us to trace the source of the external tunic of the seed, which, on account of its crustaceous or corneous texture, has been mistaken for the testa, but which is evidently of a different nature and origin.

I will also record some circumstances observed by me that may tend to throw some additional light upon the nature of this development. We very often find, in the fruits of *Rhamnaceæ*, that one of the carpels is sterile; here generally the abortive coccus grows nearly to its full size, but it is quite flattened, with its line of dehiscence, as usual, along the middle of the ventral face; in such carpels we always meet with a persistent unimpregnated ovule, standing upon its long funicle. In *Rhamnus chlorophorus*, for example, the sterile coccus is orbicular, and $1\frac{1}{4}$ line in diameter; the length of the ovule with its funicle is $\frac{5}{8}$ line; it is erect; the foramen of the primine is distinctly open, and points downward, the tunic itself showing yet no indication of any plicature; the secundine, seen through the primine is shorter and smaller; and the nucleus is much narrowed, being scarcely half the length of the primine; while the chalaza is clearly visible in the summit, and also the thick distinct opaque line of the raphe extending into it from the funicle. The position of the raphe, in this ovule, exactly corresponds with its place and direction in the ripe seed, showing, as I have before indicated (p. 81), that its situation, which has been considered abnormal in the seed, is not due to any twisting of the funicle, or to any disturbance caused by the subsequent plicature of the different parts of the ovule; and this we find to be further proved by the presence of the "telæ conductrices" immediately beneath the foramen of the primine, which would not happen had the ovule been forced round into this position by the torsion of its umbilical cord. I have found, in the several instances examined, the main line of the raphe and funicle constantly in one and the same position upon the dorsal face, everted more than the quarter of a circle (140°) from the point of zero, starting from the axial line of the fruit: from the chalazal summit, and down the contrary or ventral face of the primine, is seen a second cord, corresponding in position with the ventral raphe of the seed, and running from the summit to the mouth of the tunic. In one

l'ovule,"—an opinion which he soon renounced after his subsequent important investigations into the growth of the ovule: *Ann. Sc. Nat.* xii. chap. p. 242.

instance I traced the existence of spiral vessels for more than half the length of this cord; in another they were visible nearly as far as the foramen, but the dorsal cord was too opaque to allow them to be detected, although their presence there cannot be doubted. The stipitate funicle was about a quarter of the length of the primine, and was covered with a number of elongated transparent cells, apparently in progress of extension, in the manner observed by Brongniart, as above quoted; and to their growth and expansion we may probably look for the origin of the crustaceous coating of the seed.

I have noticed precisely the same facts in *Rhamnus Alaternus*, where the raphe is strictly dorsal, as in *R. catharticus*; in one instance I observed that the coats of the ovule had become quite opaque, the mouth of the primine being closed by a tumid expansion over it, and that this expansion embraced the long funicle, which had nearly disappeared: we may thus account for the total absence of any funicle in the ripe seed. I will not aver that this evidence is complete; but the disappearance of the funicle and the production of a distinct extraneous coating over the ovule, to whatever cause they may be owing, are most evident facts. There is much probability that this crustaceous coating derives its origin from the growth and expansion of the funicular support,—a growth first noticed by Brongniart, and apparently confirmed by what I have seen and recorded above. To this cause we may attribute the production of the vacant space that exists in the seed between the membranaceous integuments and the lower portion of the crustaceous coating, and also the appearance of the suspensor-like thread in which the base of the two membranaceous integuments terminates; for Brongniart recounts that, after impregnation, he found the mouth of the secundine embraced by the neck of the primine, just as I have described the appearance in the basal extremity of the two inner integuments of the seed of *Zizyphus*.

There exists in some instances yet another production over the seed, still more external than the crustaceous coating, the mention of which I have delayed till now. This expansion, which seems to proceed from the placental point of attachment of the funicle, shows itself in a rudimentary state in *Zizyphus*, as I have before described it, under the form of a small free cup with a crenulated margin, which remains fixed to the pericarp, and in which the sessile seed reposes: this seems to be a constant feature in that genus. In *Phylica* and its congeners the seed is affixed in a stipitate cup that remains attached to it; this is fleshy, generally four-toothed on the margin, but in one genus is deeply cleft into ten radiating lobes.

In *Alphitonia* it assumes its fullest development, appearing as

a thin, dark-coloured, brittle, submembranaceous, loose envelope, open at the top and sometimes also along the dorsal face; but in all cases the margins of this opening overlap each other, and thus entirely conceal the seed. This was first described by Fenzl*, who calls it "a brittle testa, covering the smooth cartilaginous endopleura." Endlicher†, on the other hand, designates it as an "arillus, covering a smooth corneous testa." Dr. Asa Gray‡, speaking of this tunic, "doubts if this membrane be a true arillus, as our materials are not sufficient for the complete investigation of its nature. Although marked with what seems like a raphe, it cannot be the testa or any proper integument of the seed, as Fenzl (in Pl. Hugel) took it to be, for it has no connexion with the corneous seed-coat at the chalaza, but only at the hilum; the chalazal end appears to be slightly open, as would be the case with an arillus: perhaps this membrane is a separable lining of the coccus."

I have not been able to detect the presence of any kind of vessels in this tunic, particularly in the prominent line that "seems like a raphe," and which Endlicher positively calls a raphe: this prominence appears to me nothing more than a mere impression of the sutural line of the coccus, and is a common feature seen upon the corneous coating of the seed in the *Colletieæ* and other Rhamnaceous genera. The tunic certainly presents all the characters of an arillus; and, as Dr. Asa Gray justly remarks, it cannot be one of the proper integuments of the seed. The hard seed of *Alphitonia* is perfectly sessile within it, and is attached to it by a small open transverse fissure in its base, as in *Zizyphus*.

Other circumstances, however, present themselves in the organization which I have found in the seed of *Alphitonia excelsa*, that are worthy of record, as they completely confirm all the details of structure previously described, and which seem to prevail throughout the *Rhamnaceæ*. The second hard tunic, which lies within the outer brittle coating last described, becomes softened by maceration, when it is easily detached; it is then very lax, is of a pale-brown or yellowish colour, quite homogeneous in texture, void of any vessels, and encloses an oval body covered by a third tunic, which is notably smaller in size, and therefore leaves a considerable vacant space all round its sides and its summit, and is connected with the second tunic only at a small point in the base, which corresponds with the basal slit in the outer tunic of *Colletia* and *Zizyphus*. The summit of this third tunic is marked by a large tumid spot, evidently a chalaza, which exhibits no indication of any previous connexion with the

* Plant. Hugel, p. 20, sub *Colubrina excelsa*.

† Gen. Plant. no. 5712.

‡ Bot. Explor. Exped. Un. St. p. 278.

second tunic; along each margin, emanating from the basal point of attachment, and crossing over the chalaza, there is seen a prominent white cord, filled with spiral vessels, which is imbedded in the fleshy tissue of the integument, in one continuous and completely peripheral line, exactly like that described in *Colletia* and *Zizyphus*. Within this tunic is yet a fourth, delicate integument, a thin albumen, and an embryo similar in form to that of *Colletia**.

I have abstained from giving any denomination to the seed-coats in the foregoing descriptions; but we may now enter into this inquiry. In regard to the two inner coatings, no doubt can be raised against the obvious conclusion that the innermost is the tegmen produced from the secundine of the ovule, and that the other, in which the raphe is imbedded, is the true testa; developed from the primine, notwithstanding its soft fleshy texture. What, then, is the nature of the outer hard corneous coating in *Colletia*, the external crustaceous covering in *Rhamnus*, and the second tunic in *Alphitonia*? for there can be no doubt that they are all similar in their nature, and all derived from the same origin. The larger size of this tunic in *Alphitonia*, its lax condition in regard to the testa which it envelops, the total absence of any cicatrix or mark that could indicate any previous connexion with the chalazal disk of the testa, are circumstances that manifest a distinct and subsequent origin. Indeed we have seen the proof of this in the seeds of *Rhamnus* (*ante*, p. 89), where in the same fruit we have found fertile and sterile carpels: in the latter case, the spiral vessels of the raphe were imbedded in the substance of the outer tunic of the ovule; in the former case, this raphe was found only in the second coating of the ripe seed: another adventitious coating, perfectly deficient of vessels, in the interval of growth had thus manifested its existence, apparently developed from the fleshy funicle which had simultaneously disappeared. This adventitious coating must therefore come within the category of an arillus. In such case the question presents itself—what is the nature of the outer brittle tunic in *Alphitonia*? Is it also an arillus, and have we in this genus two distinct arilli enveloping its seeds? The truth of this conclusion, at first sight, appears subject to little doubt.

On the other hand, I must not omit to record an instructive fact that I have observed in the fruit of *Alphitonia excelsa*. The fruit consists of three carpels, and, in the instance examined, only one of these contained a perfect seed; the two sterile carpels presented a single erect ovule, each being half the length of

* The details of structure of the ovule and seed of *Alphitonia* will be shown in plate 33 F of the 'Contributions to Botany.'

the carpel; the ovule was of an oval form, it had become thick and opaque, its foramen was closed, and it was sessile within a short cup, with a lax undulating border, that was borne upon a solid stipitate support, of the same length and diameter as the body of the ovule. This was evidently an early stage of growth of one of the two arilliform coats of the seed, but whether of the inner or outer one, it is not easy to determine.

I have here suggested the probable assumption that the hard corneous seminal coating in *Colletia*, and the crustaceous covering in *Rhamnus*, derive their origin from a growth of the funicle—an assumption strengthened by the original observations of Brongniart; but it might possibly be argued that this coating is developed from the primine of the ovule, simultaneously with the intermediate tunic in which we find the double raphe-like cord, in the same manner as has been contended, in the case of *Magnolia* (which I have endeavoured to show has been contested upon erroneous grounds), that these two tunics form a compound testa, both developed from one single ovular coating, the primine. Against this supposition, in the case of *Rhamnaceæ*, many serious objections present themselves, in addition to those I have elsewhere advanced*:—1. No trace of vessels of any kind is found in the outer coating. 2. There is no scar or other mark upon the apex of this outer coating, to indicate its previous attachment to the chalaza of the intermediate raphigerous tunic; on the contrary, there is always a considerable vacant space between that summit and the chalaza. 3. In many species of *Rhamnus*, this external crustaceous covering does not form an entire coating, but is open from top to bottom, as an enfolded flat plate would be: this could not possibly happen if it were a resilient portion of the growth of the primine. 4. In the ovule, we find a long funicle supporting it, which disappears altogether in the seed. 4. This disappearance of the funicle takes place very soon after the period of impregnation of the ovule, when it becomes lost within a thickening around the micropylar extremity of the primine, which is then enclosed by it, apparently as if this thickening, and the formation of the outer crust, proceeded from an expansion of the funicle. We may hence draw the almost certain conclusion that this external seminal tunic is of adventitious origin, and of a distinct growth, subsequent to the period of the fertilization of the ovule.

In regard to the yet more external brittle covering of the seed of *Alphitonia*, there appears no sufficient evidence to indicate the precise source of its origin with any degree of certainty; but the facts I have already recorded concerning the sterile car-

* Linn. Trans. xxii. 86; Ann. Nat. Hist. 3 ser. i. p. 280; *ibid.* ii. p. 185; *ibid.* iii. p. 132, note, and pp. 144, 145, note.

pels are of some value towards this end. It may be argued, as indeed it has already been suggested by Dr. Asa Gray (*ante*, p. 91), that this covering may belong to the pericarp, and not to the seed. This suggestion, however, may be regarded under two distinct points of view: the covering may be considered either as consisting of a resilient portion of the endocarp, or as a separate development formed within it, analogous to the ordinary arilliform productions around seeds. The former view conforms with the suggestion of Dr. Asa Gray, and coincides with the line of argument adopted by him in regard to the seed-coats of *Magnolia*, to which I have just alluded; and upon this supposition, the brittle covering of the seed of *Alphitonia* would consist of the endodermal lining of the endocarp, which becomes separated from it under the form of a resilient membrane. We have, however, strong evidence to prove that no such occurrence has taken place; for if it had, this tunic ought to exhibit on its ventral face the same sutural line of dehiscence that the endocarp does; on the contrary, we find the ventral face of that tunic perfectly entire, though marked by the impression of the hollow sutural line of the endocarp; and we notice an aperture in its apex, often continued some way down the dorsal face, and that this opening does not form a sutural line, but that its margins are sinuous and overlap each other. It is therefore quite manifest that, if this tunic belong to the pericarp, it cannot be any resilient portion of the endocarp.

Under the second mode of viewing this question, that it is a distinct formation, much evidence, in the way of analogy, may be drawn from other well-known cases; but I will refrain from entering into this consideration at present, as I shall on a future occasion discuss the nature of other adventitious coatings within the pericarp of seed-vessels, which seem to originate in peculiar depositions, or from the growth and expansion of the placental surface. Among the many kinds of development of this class, which seem to have attracted little notice, may be mentioned the pulpy sacs in which the seeds of *Cucurbitaceæ* are severally enveloped, each sac being attached to a distinct bundle of tracheal vessels branching from the broad placental laminæ, as described by St.-Hilaire*, where these pulpy sacs are at first solid and fleshy, and afterwards become liquid and mucilaginous. A very similar growth is developed from the placental plates of the fruit of *Adansonia*, where a thick deposit is formed around each seed. *Leguminosæ*, too, offer numerous examples of analogous growth. The large ball of elastic silky hairs that envelope the seeds in *Bombax* and other kindred genera derives its growth wholly from the pericarp, and not from the seeds. In *Hydro-*

* Mem. Mus. v. 306.

phyllum and *Ellisia* (Gærtn. pl. 110 & 184), the placenta grows round the seeds, which it soon encloses entirely, and fills the cell of the fruit. When the capsule bursts, this looks like an internal coccus, assuming the appearance of a resilient endocarp, which opens into two valves corresponding with those of the capsule; and upon the inner surface of these placenary valves the seeds are parietally affixed.

[To be continued.]

IX.—On *Clostophis* and *Rhiostoma*, new Burmese Genera of Land-Shells. By W. H. BENSON, Esq.

*Clostophis**, B., nov. gen.

Testa sub-biconica; anfractus penultimus maximus, ultimus descendens, solutus, subaxialis, minor; apertura integra (specie adhuc cognita), dentata.

C. Sankeyi, B., n. s.

Testa late umbilicata, sub-biconica, lævi, spira turrito-conica, lateribus cavis, apice obtuso, sutura profunda; anfractibus 5, primis angustis convexiusculis, penultimo multo majore cylindrico, ultimo antice rapide descendente, soluto, tubuliformi, quoad peripheriam antepenultimi minore; apertura integra, subaxiali, subumbilicali, valde obliqua, subcirculari, intus superne dente 1 submarginali loco quasi parietali munita, peristomate tenui, expanso.

Diam. major $1\frac{1}{2}$, alt. $1\frac{3}{4}$ mill.

Habitat prope Moulmein, ad cavernas "Farm Caves" dictas.

I discovered this singular shell in the earth which filled the cavity of a decayed specimen of *Sophina schistostelis* collected by Major R. H. Sankey. It was accompanied by a minute and new species of *Hydrocena*. The specimen is weathered. Notwithstanding the presence of a tooth in the aperture, there is little room for hesitation in referring this novel form to the *Cyclostomacea*, with reference to the solute descending last whorl, and to the entire subcircular aperture, the expanded margin of which forbids an union with *Aulopoma*, from the impossibility of its being furnished with a similar operculum; while the absence of a slit and crowning tubular process prevents association with *Rhiostoma*. That the presence of a tooth within the aperture does not militate against Cyclostomaceous affinity is demonstrated by its occurrence in the genus *Diplommatina*†.

* κλωστός, coiled; ὄφις, serpent.

† In the Brazilian *Cyclostoma disjunctum*, Moricand, the solute last whorl descends laterally, as in *Aulopoma*.